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ON THE GENERA OF THE DIPNOI DIPNEUMONES.

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The Dipnoi are a group of piscine vertebrates, unusually interesting, alike to the morphologist, the paleontologist and the physiologist. Hitherto these animals have proved, in many respects, unsatisfactory objects of study, since the existing forms have been accessible to but few workers, and then only as more or less poorly-preserved alcoholic specimens. Only within the last few years has this condition of things changed so that quite recently our knowledge of this group has been enriched by many interesting and important additions to the morphology, physiology and the general biology of two of the members of the group representing the two commonly accepted genera.

The papers containing the results of the researches upon the living specimens of *Lepidosiren annectens* we owe to Professor J. Waldschmidt, who has worked out the Dipnoan brain from the comparative standpoint, and in histological detail, and to Professor W. N. Parker, who has studied in more or less detail almost all of the organs of the body except the skeletal and nervous systems. His study was directed to the solution of the numerous points left unsettled by previous workers who were less favored in the quality of their material, and not to a fundamental research into the nature and relationships of any

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of the organs of the body. Professor Parker has gone over the ground covered by my paper on the anatomy and physiology of the Dipnoi,[2] and has cleared up some of the things which I was unable to carefully study, owing to the fact that the only material accessible at that time consisted of store-bought alcoholic specimens, intended, without doubt, for museum collections. Hence, it not unfrequently happened that questions depending upon histological detail could not be satisfactorily or finally solved. On the other hand, Parker has arrived at some conclusions which I think are hardly justified in the present state of our knowledge, and it is to these matters that we will now confine our attention. In my Freiburg paper I suggested that it was hardly permissible to maintain two distinct genera of the Dipneumones, and I based my suggestion upon the lack of adequate structural differences between the forms commonly held to be generically distinct. I proposed on that account to use the name *Lepidosiren* instead of the name *Protopterus* for the African species, and I called attention to the great scarcity of the individuals of *Lepidosiren paradoxa* in museum collections.

My remarks, and more especially the adoption of the name *Lepidosiren* as the sole genus of the *Dipneumones* had the effect of calling out a reply from the late Professor Anton Schneider, of Breslau,[3] and also an article by Dr. George Baur,[4] of Chicago University.

Quite recently, Parker publishes his agreement with the conclusions of Schneider and Baur as far as the generic distinctness of the African form is concerned. It may be of interest to the uninitiated to know that none of the recent writers have ever seen a fragment of a *Lepidosiren paradoxa* from South America, and we all alike depend upon the published accounts of this creature's anatomy by Bischoff, Hyrtl, Klein, and a few others, all of whose investigations were made on two or, at the most, three animals, and some of the workers had at their disposal for study only the material which had already been dissected by their predecessors, e. g., Hyrtl. Their papers were published some years ago (in the 40s or 50s), and leave much

to be desired when examined for the solution of the problems of to-day.

Schneider's paper was based upon original investigation of a considerable number of African mud-fish from several widely-separated localities, and his conclusions are that *Protopterus* is not only generically distinct from *Lepidosiren*, but that there are also two well-defined species of the African form, to be separated on account of the number of ribs, the presence or absence of the cartilaginous fin-rays and some other characters of no importance here. Baur's paper is an historical resumé of the main facts about *Lepidosiren paradoxa*. In general, however, the reasons which have been given for keeping *Protopterus* distinct from *Lepidosiren* may be concisely stated as follows:

1. The presence of 4 gill-holes in *Lepidosiren* and 5 in *Protopterus*.
2. The presence of a larger number of ribs in *Lepidosiren*.
3. The absence of fin-rays in *Lepidosiren* and their presence in *Protopterus*.
4. The absence of external gills in *Lepidosiren* and their presence in *Protopterus*.

I shall now endeavor to show that the critics of my suggestion of the generic identity of these two forms have failed to bring any proof that it is not entirely reasonable and highly probable, and by their own investigation have weakened their case by discovering facts which go to prove the close relationship of these animals.

THE GILLS.

All the writers on this subject have failed to see the important agreement between the gill structures of *Lepidosiren* and *Protopterus*, and have been led off to base important conclusions on a relatively unimportant point in their anatomy. The statement which Schneider and Baur base so much upon, viz.: that *Protopterus* has 5 gill-slits, while *Lepidosiren* has only 4, certainly looks important enough to give the advocates of a

genus apiece for these creatures ample warrant for their conclusions; but when we examine the actual significance of this difference in the number of holes in the side of the neck, most if not all the value of this character is destroyed, for the number of functional gills is the same in both animals.[5] The facts are that both animals have 5 gill-bars, but only $2\frac{1}{2}$ gills; that the first and second gill-clefts are in both forms devoid of a respiratory membrane or structures, although their secondary blood supply through the bronchial artery still persists. These two pair of gills are completely atrophied in both creatures physiologically since they no longer serve in respiration, and the denuded slits are subject to that variation which is the fate of all rudimentary organs. The first slit suffers most and is greatly reduced. In the two (or three?) specimens of *Lepidosiren* which have, up to date, been dissected, the edges of the slit seem to have grown together, while in *Protopterus*, though the slit is still open, it is very much reduced, being smaller than any of the other gill slits. I venture to say that no very large number of individuals of *Protopterus* have been examined with special reference to this point. However that may be, the coalescence of the walls of a degraded gill-slit is not a character of sufficient morphological importance to found a genus upon, except, perhaps, in the eyes of a confirmed genus builder.

In both forms neither the first nor second gill-bars bear any gill membranes, but both possess an hyoidean demibranch (opercular gill rudiment). This gill is composed of a single row of gill leaflets as in *Ceratodus*. The third and fourth gill bars are provided with a double row of gill leaflets, while on the fifth arch is found only a single row of leaflets, a condition not obtaining in any other *Dipnoan* or *Ganoid*.

When these animals were named, they were little known to science. If they had to be named as new discoveries to-day, and could both be studied together in so doing, most zoologists would include both animals in one genus, even if they did not group them as varieties of one species.

I wish to call the attention of those anatomists who would insist upon keeping *Lepidosiren* and *Protopterus* distinct upon

the basis of the number of gill clefts left open irrespective of the fact that the number of functional gills is the same, to the fact that there are other fish with a variable number of gills which are considered by as good authority as Johannes Müller, to the extent of his knowledge of the case, to be *mere varieties* of *one species*. Müller found among the *Bdellostomæ* from the Cape of Good Hope, individuals with 6 pairs of gills, others with an extra gill added to one side of the body, and still others with 7 full pairs of gills.

I have ascertained that, taking all the *Bdellostomids* together, they form a series in which the gill variation runs between the minimum of 6 pairs and the maximum of 14 pairs, or a DIFFERENCE BETWEEN THE EXTREMES OF 8 PAIRS OF GILLS, AND YET ALL THESE INDIVIDUALS NOT ONLY BELONG TO THE SAME GENUS—THEY BELONG TO THE SAME SPECIES!

THE RIBS.

The number of ribs has been selected by Schneider as a character of *generic* as well as specific value. The possession of 56 ribs is held to be characteristic of *Lepidosiren parodoxa*. Considering the small number of individuals examined, this cannot justly be said to be a settled fact. Schneider's diagnosis of 30 ribs for *Protopterus amphibius*, and of 35 ribs for *P. annectens* as a safe specific character, is, to say the least, ill-chosen, for the reasons that the number of ribs varies in specimens from the same locality, which have no other distinguishing characters save another variable, viz.: the presence or absence of external gills, and for the further reason that some authors (Owen, loc. cit. p. 47) have counted at least 37 ribs in *P. annectens*. Schneider failed to define what structures he would have counted as ribs; but I assume he would admit all rib-like processes attached to the bare notochord between the pectoral and pelvic girdles as entitled to be named ribs irrespective of questions of homology. THE NUMBER OF SUCH PROCESSES IS INCONSTANT IN *Protopterus*, but the extremes of variation have not been definitely made out. The number probably varies with age, but this is not certain.

Parker[6] has shown that Schneider's second species of *Protopterus, P. amphibius* is a mistake. Schneider gives the Gambia as the habitat of this species. The distinctive characters separating this species from *annectens* are the presence of lateral cartilaginous rays in the fin membranes and only 30 ribs.

Schneider describes the fins of the *Protopterus* material which Peters brought from Quellimane as long and pointed, but flattened appendages. This was found to be true of the pectoral fin, the pelvic fin being thickened at its base. The cartilaginous axis of each fin bears on one side several cartilaginous rays which support the membranous border of the fin. This border is, in turn, stiffened by numerous horny filaments (horn-rays). This membrane is found on the ventral edge of the pectoral fin. Schneider found cartilaginous rays in *P. amphibius* only.

Parker states that his animals were from the Gambia, and that the specimens which he "examined for the purpose possess in the middle part of the fin, numerous cartilaginous parameres on each segment in both fins," which, according to Schneider, is one sure sign of *P. amphibius*, but Parker's animals also had 35 ribs, which is one of Schneider's marks of *P. annectens*. Parker concludes that there is possibly considerable variation in both these structures within the species, and this agrees with what Wiedersheim has previously found with respect to the FIN MEMBRANES, irrespective of their supporting structures.

EXTERNAL GILLS.

Owen,[7] McDonnell,[9] Schneider,[3] Wiedersheim,[14] Peters and Parker[6] describe or mention the existence of external gills in specimens of *Protopterus* from the different localities of Africa. Owen's observation has already been referred to. McDonnel simply states that he found three processes, rudimentary external gills the longest of which measurd 4‴.

Boas makes the following statements concerning the external gills of the African mud fish.

" Uber die sogenannten äusseren Kiemen von *Protopterus* müssen wir ein Wort sprechen. Die betreffenden Gebilde waren bei den zwei von mir untersuchten *Protopteri* sehr klein,

offenbar ohne jegliche Funktion. NACH PETERS SIND SIE DAGEGEN BEI JUNGEN EXEMPLAREN STÄRKER ENTWICKELT. Ich glaube dass man diese organe . . . . am richtigsten, oder wahrscheinlichsten, in die Reihe der vielfachen accessorischen Athmungsorgane, die wir bei Fischen finden, stellt. Ich finde es ferner sehr zweifelhaft, ob sie etwas mit den äuseren kiemen von *Polypterus* gemein haben die anderen Ursprungs, anderen Baues ist und von anderun Blutgefässen versorgt wird."

The branchial blood-vessels, as described by Peters and Owen (for *Protopterus*), are very different structures.

Parker found external gills in all of the specimens examined by him, but his largest were still comparatively small animals. He quotes Peters as finding them on fish 2–3 feet long, and that in young specimens they are thinner, while in old specimens they are broader. Parker asserts that my statement that these gills are only present in young animals is certainly incorrect. Boas quotes Peters as above, which is not in harmony with Parker's use of Peters' words. The majority of writers on this point agree that they belong to small or young animals, as is the case with the gills of *Polypterus*, and Parker's material was not sufficient to add anything to the settlement of this question.

With reference to the food habits of *Lepidosiren annectens*, there is no longer any doubt as to its omnivorous tastes.

Professor Parker has shown that it may, at times, be cannibalistic, but he errs in supposing that I maintained that it had entirely changed its food habits. Starting from supposed carnivorous ancestors, I claimed that *Ceratodus* had become essentially herbivorous in its habits, while *Lepidosiren* had only partly modified its habits in this respect. On page 510 of my Freiburg paper, Professor Parker might have read: "Der Darm ist bei Ceratodus stärker verändert, als bei *Lepidosiren*, und diese Verschiedenheit correspondirt mit der Grösse der veränderung, die Function erfahren hat," and further, that "Das Futter des Ceratodus besteht gegenwärtig aus verschiedenen, kleinen Mollusken (reichliche Schale von Gasteropoden und Lamellibranchiaten fanden sich im Darme), Gras, Riethgras und Zahl-

reichen anderen Pflanzen stücken." And I further ascertained that while the plant remains were not masticated, the shells had all been crushed to fragments. Now, if *Ceratodus* eats animal food, and has been modified more than *Lepidosiren* in the direction of herbivorous diet, it follows that *Lepidosiren* is also partly carnivorous.

The quotation which Parker makes from my paper, referring to the breeding habits of the Dipnoi, applies to *Ceratodus* only, and not in any part to *Lepidosiren*, and the trouble arose in the transposition by the printer, of the reference number which occurs in my MS. after the word "Beobachtung," to the next line of the printed text. The transposition escaped correction in the proof. The authority for the statement is, to the best of my recollection, *The Zoologist*, 3d Ser. Vol. VII, 1884 (?).

After a study of the pectoral fins, to which Professor Parker devoted his special attention, he concluded that they do not serve the function of feelers. This conclusion is not well-grounded, for it rests upon the author's failure to find tactile SENSE ORGANS in the skin of the appendages. Our author remarks "that the nerve supply seems out of all proportion to the rudimentary muscles, and this fact renders the absence of sensory organs all the more surprising," and, on p. 124, "So far as I have been able to observe, *all* the sensory organs in connection with the epidermis have the form of the 'lateral-line organs' described above, and in this point therefore, as in many others, *Protopterus* resembles amphibians more than fishes," a conclusion which, will without doubt prove to be too lightly drawn, for from the knowledge which we possess of nerve endings in the skin of fishes, and the methods of demonstrating them, it should not be a very difficult matter to show that the large nerve supply is, in this instance, distributed to the epithelium of the pectoral appendages in its character of a sensory apparatus.

The nerve supply indicates that the brachial nerve must contain many sensory fibers. It is composed of the first three spinal nerves, the dorsal and ventral roots of the hypoglosal, and a branch of the vagus. There is every evidence that the appendage is a very sensitive tactile organ, and the nerve-end

apparatus will be found by making a proper study of the skin.

Referring to the occurrence of taste-buds in the *Lepidosiren annectens*, Parker states that I have described somewhat similar organs on the palate of *Ceratodus*. As a matter of fact, the description I gave applied to both *Ceratodus* and *Protopterus*, though I figured the organs from *Ceratodus* alone. I am pleased to see that Parker is able to confirm my own observations in this respect.

Hyrtl states that the intestinal canal of *Lepidosiren paradoxa* is slightly S-haped in the horizontal plane.

In *Ceratodus forsterii* and *Lepidosiren annectens* I found there was no indication of curvatures in the horizontal plane; but Parker states that he finds the gut in *L. annectens* slightly curved (S-shaped) in the VERTICAL plane, and hence that my statement that the alimentary tract in the Dipnoi is strictly parallel with the notochord is incorrect.

Even Parker's observations show the correctness of my statement, while he says, on page 215, "The alimentary canal extends almost in a straight line from the mouth to the vent," making no mention of curves.

The sensory papilla which I found projecting as a finger-shaped process part way across the anterior narial opening in *L. annectens*, Parker was unable to detect. No histological examination was made of this papilla, but I judged it to be tactile in function and from its location to serve as a guard to the entrance of the nasal chamber.

Our author does not produce any evidence for the support of his change in the name of the URINARY BLADDER to that of the CLOACAL CÆCUM, and he adds nothing to our knowledge of either its structures or its functions, so that any comparison of this organ with the rectal gland of Elasmobranchs is entirely against the known morphological relations of the two organs. The rectal gland of Elasmobranchs is a diverticulum of the gut in close relation with the end of the spiral valve, while the urinary bladder of the Dipnoi is a pocket of the cloaca entirely foreign to the gut, since it lies outside of the rectal sphincter and in close relation with the openings of the kidney ducts.

With regard to the LYMPHOID ORGAN of the mid-gut, which

was fully described in my paper, Parker thinks he has positive evidence that it is a spleen, and hence uses this designation throughout. The name was first applied to this structure by Klein. The term spleen in anatomy is used to designate a definite body of lymphoid tissue which is usually more or less closely connected with some part of the mid-gut, though it may lie in the mesentery far from the walls of the gut. The name is strictly morphological in its bearing, and does not carry with it the idea of specific and localized functions. So far as the mass forms a discrete body, the term spleen is appropriately applied to it, for it serves to definitely mark the mass, but when the mass is absent, or, in other words, when the tissue has other relations, e. g., as in the Dipnoi where it is inclosed WITHIN the wall of the gut, we not only do not gain in the accuracy of designation, but we detract from the definiteness of the name as applied to other forms.

In structure, these tissues are not to be distinguished from each other, and if the aggregation in the region of the mid-gut is to be called spleen, those in the hind-gut and fore-gut are likewise spleens. We avoid difficulties of nomenclature if we reserve the term spleen for a discrete mass of lymphoid tissue which lies in the mesentery outside of the walls of the mid-gut.

Professor Parker has done a great service in tracing out the extent of the pancreas which, in the Dipnoi, lies entirely within the walls of the gut between its two coats and which he has described in histological detail for the first time; but the discovery of the pancreas and its ducts was made by McDonnell in 1858. This investigator made observations on living material which was afterward used for dissections, and he clearly states that the pancreatic ducts empty into the mid-gut in company with the bile ducts. Melville added a note to McDonnell's paper to the effect that both spleen and pancreas were present in the organ which the latter called pancreas.

No one has yet pointed out the very great significance which the condition of the pancreas in *Lepidosiren* has from a comparative anatomical standpoint. It is by far the most primitive condition of the organ known for the VERTEBRATA, since it

remains entirely within the intestinal wall lying between the mucous membrane, of which it is an outgrowth, and the muscular coat of the gut and it thus represents a very early stage in the ontogency of the organ as it is developed in other animals.

Professor Parker states that the spiral valve in *Lepidosiren annectens* makes 6 or 7 turns. I found in all the specimens studied, and the point was specially examined, that the number was uniformly eight.

Our author attributes the statement to me that *Lepidosiren* lacks a distinct muscular coat to its stomach, and that in the intestine the musculature is only slightly developed.

On page 491 of my "Beiträge" I state: "Sowohl bei *Ceratodus* als bei *Lepidosiren* sind die Wände des Vorderdarmes auffallend dünn. Bei der maceration traten zwei deutliche Lagen von Muskelzellen hervor. Sie repräsentiren die Längs- und die Ring muskulater der höheren Wirbelthiere und sind sehr ähnlich der Muskelelementen der Cyclostomen, etc."

The passage which Parker alighted upon to misconstrue by taking it away from its context, reads as follows: "Bei *Ceratodus* ist das *Magenende* veshältnissmässig viel weiter als bei *Lepidosiren* (italics inserted here). Eine deutliche Muskulatur fehlt, doch sind zahlreiche spindelförmige Muskelzellen durch das ganze Bindegewebe der submucosa zerstreut."

Parker states that he failed to find the lobulation of the kidneys in *Protopterus* as described by me for the older individuals. My observations were made on a specimen 42 cm. long. The lobules were well-marked, but not so numerous or so sharply defined as in *Ceratodus*. He concurs in my statement that the so-called male organs of writers previous to 1884, were, in all probability, only immature female organs. Parker describes the presence of two vibratile filaments in the spermatozoan of *Protopterus* and considers this condition unique among vertebrates. I have observed the same structure in ripe spermatozoan of *Rhinoptera bonasus*. My observations were made on July 13, 1889, at the Marine Biological Laboratory, and it was found that the apparently single-headed, double-tailed spermatozoan resolved itself into a simple, straight filament, possess-

ing a thickened body in the middle with a tapering filament given off from either end of it. The only difference between the two ends of the central body of the sperm-cell was the presence of the nucleus at one end from which the longer filament was given off. During life, both of these filaments are spirally but loosely coiled about one another, and during progressive motion this arrangement gives rise to the appearance of a vibratile membrane spirally placed on the tail. On adding Perenyi's fluid to the sperm, the cells, one and all, flew out straight and rigid, and the refractive body (nucleus ?) became very distinct in each. I have observed this structure in other fish spermatozoa, but never so distinctly marked as in the cow-nosed skate. It is possible that the double tail of *Protopterus* will be found to be constructed after this plan.

Owing to the very great scarcity of specimens of *Lepidosiren paradoxa*, it may be of interest to many to have a list of the known examples with their present resting places.

The following is a table of all the South American specimens of *Lepidosiren* yet taken and recorded:

Specimen	Discovered by	Locality.	Size.	Condition.	Museum.
No. 1	Natterer	Borba on the R. Madeira, 1836.	3 ft. 9 in.	Dissected	Vienna
No. 2	Na terer	Villa Nova on the R. Madeira, 1836.	1 ft. 10 in.	Dissected	Vienna
No. 3	Unknown	Unknown, 1840.			Paris
No. 4	Castelnau	Ucayali River, 1847.		Dissected	Paris
No. 5	Dr J. Barbosa Rodriguez	Igrapé de Aterro, (Manáos), 1886.	in cm. 85, female	Whole	Florence, Italy.
No. 6	Rodriguez	Autaz, Madeira River, '87	in cm. 40	Whole	Florence, Italy.

The fifth specimen was a female with well-developed eggs, which was caught in August, 1886. It was 85 cm. in length, and 28 cm. in girth at thep ectoral appendages. The body is distinctly cylindrical in shape, but somewhat flattened on the abdominal surface where the scales are bigger, thicker and lighter in color. The tail is short and much compressed, and is provided with an irregularly-rounded caudal fin, which is not continued cephalad as a true median fin, but only as a slight keel to the middle of the back. The fin rays of the caudal portion are

cartilaginous. The pectorals and pelvic appendages lack a membranous edging. The pectorals are slender and compressed, while the pelvic appendages are stouter and conical in shape.

The scales are disposed in longitudinal rows, 10 in each, and are of a dark brownish purple color, with distinct blotches except on the belly. The lateral line is double. The eyes are small and lie beneath the skin. The branchial openings are very narrow, and are protected by thick fleshy flaps. External gills are absent, and the internal gills cannot be seen through the deep and narrow branchial slit. The mouth has fleshy lips. The gill-clefts are four in number, the fourth being much reduced. The three free branchial arches are fringed with conical papillae. The cloacal opening lies 10 mm. to the left of the median ventral line.

The sixth specimen comes from the same hands, and is in the Florence Natural History Museum.

It is much to be desired that these well-preserved specimens may become the means of clearing up many points in our account of the anatomy of the Dipneumonous Dipnoi.

[2] Jenaische Zeitschrift Bd. XI, 1885.

[3] Schneider, A., Uber die Flosen der Dipnoi und die Systematik von *Lepidosiren* und *Protopterus*, Zoologischer Anzeiger, No. 231, 1886.

[4] Baur, G., *Lepidosiren paradoxa*. Zoologischer Jahrbücher, II, 1887.

[5] The following notes on the statements given by different authors may be of interest in this connection:

Wiedersheim (Lehrbuch, p. 608) says *Protopterus* has 6 gill-bars and 5 gill-slits, with three and one-half gills.

Owen (Comp. Anat.. p. 468–481, '82, '85, '86) gives the same number of gill-bars, but says that there are 2 biserial, and 1 uniserial gill, besides which there is the opercular gill attached to the membrane supported by the hyoid. That "three seemingly analogous filaments (i. e., analogous to the embryonic external gills of Elasmobranchs) are retained on each side for a longer period in *Lepidosiren annectens*, but lose their vascular and respiratory character before they are absorbed."

Parker gives (Trans. Roy. Irish. Acad., V. 30, pt. 3, p. 161) 5 gill-bars and 4 gill-clefts, exclusive of the spiracle or hyobranchial.

There is a difference of one gill-bar between Parker and all other observers. There is a further discrepancy among observers as to the number of gills. In the case of *Lepidosiren paradoxa*, Bischoff and Hyrtl disagree as to the number of hemibranchs, the former describing the same arrangement of gills for *paradoxa* as exists in *annectens*, but Hyrtl, who worked over the same specimens, says that the gill-plates are absent on

the first and last arches, only a trace of them being observable on the fifth. Since Hyrtl studied the material after Bischoff had dissected it, it seems probable that these gill filaments, being tender in nature, were broken away during the previous study, leaving only the "fadenförmigen Zotchen" found by Hyrtl.

[6] Parker, W. N., Anat., Physiol. of *Protopterus*, Trans. Irish Acad., 1892.

[7] Owen, R., Comp. Anat. Vertebrates and Description of *Lepidosiren annectens* Trans. Linn. Soc., XVII.

[8] Giglioli, *Lepidosiren paradoxa*, Nature, 1892.

[9] McDonnel, Anatomy and Physiology of *Lepidosiren annectens*, 1854.

[10] Bischoff, Th. L., *Lepidosiren paradoxa*, Leipzig, 1840.

[11] Hyrtl, J., *Lepidosiren paradoxa*, 1845.

[12] Klein, Beiträge zur Anatomie d. *Lepidosiren annectens*, Jahrb. d. ver. f. Naturk. in Würt., 1864, XX.

[13] Burckhardt, R., Das Nervensystem der Dipnoern (*Protopterus annectens*) 1892.

[14] Wiedersheim Grundriss der vergl. Anat. 2te ed. 1893.